

**FINAL REPORT FOR JOINT VENTURE PHASE 1 BETWEEN U.S.  
DEPARTMENT OF AGRICULTURE, FOREST SERVICE ROCKY  
MOUNTAIN RESEARCH STATION WORK UNIT 4152 AND  
REGENTS OF THE UNIVERSITY OF COLORADO**

**FOREST SERVICE AGREEMENT: ~~00-JV-11221605-221~~**

211

**June 1, 2001**

**Yan B. Linhart and Kailen A. Mooney  
Department of EPO Biology  
University of Colorado, Boulder**

**PROJECT TITLE: The effects of multiple predators on ponderosa pine canopy herbivores and dwarf mistletoe demography.**

**SUMMARY**

This document is the final report of Phase 1 for Joint Venture: 00-JV-11221605-221 between the USDA Forest Service Work Unit 4152 and the Regents of the University of Colorado. In this document, as called for in the Joint Venture Agreement, we provide the following: (1) A summary of the work completed during the period encompassed by Phase 1 as described in the Work Plan submitted to the Forest Service on October 17, 2000, and (2) A description of field studies and other related tasks to be conducted during Phase 2 of the Joint Venture.

**A. INTRODUCTION**

Ponderosa pine (*Pinus ponderosa*) has the largest geographic range of any conifer in North America (Baumgartner and Lotan 1988). Ponderosa pine ecosystems dominate much of the montane West, and are of tremendous ecological and economic importance. Parasites and herbivores pose formidable challenges to plant fitness generally (e.g. Howe and Westley 1998; Fritz and Simms 1992), and to ponderosa pine specifically (Furniss and Carolin 1977; Baumgartner and Lotan 1988; Hawksworth and Wiens 1996). Innate resistance represents one important line of defense against such natural enemies (Howe and Westley 1988; Fritz and Simms 1992). A second and perhaps equally important source of protection is provided by those predators that keep such natural enemies in check according to the adage that "the enemy of my enemy is my friend" (Hairston et al. 1960). The goals of the research for this Joint Venture has been to investigate the effects of predators on ponderosa pine herbivores and to investigate how parasite-induced changes in ponderosa pine morphology affects the assemblage of arthropod predators residing in pine canopies.

The efficacy of predators as protectors of plants likely depends on many factors, the most important of which may be the composition of the predator assemblage. Predator assemblages vary in the protection they provide plants from herbivores because individual predator taxa can vary in effect strength. In addition, interactions among multiple predators in an assemblage can change their combined effect strength such that as an assemblage, predation strength may be greater or less than the sum of the predator's individual effects (Sih et al. 1998).

We are conducting two separate lines of inquiry investigating predator assemblages in ponderosa pine forests. Southwestern dwarf mistletoe (*Arceuthobium*

LINHART, Y. B.

2001

**FINAL REPORT FOR JOINT VENTURE PHASE 1 BETWEEN U.S.  
DEPARTMENT OF AGRICULTURE, FOREST SERVICE ROCKY  
MOUNTAIN RESEARCH STATION WORK UNIT 4152 AND  
REGENTS OF THE UNIVERSITY OF COLORADO**

**FOREST SERVICE AGREEMENT: ~~00-JV-11221605-221~~**

211

**June 1, 2001**

**Yan B. Linhart and Kailen A. Mooney  
Department of EPO Biology  
University of Colorado, Boulder**

**PROJECT TITLE: The effects of multiple predators on ponderosa pine canopy herbivores and dwarf mistletoe demography.**

**SUMMARY**

This document is the final report of Phase 1 for Joint Venture: 00-JV-11221605-221 between the USDA Forest Service Work Unit 4152 and the Regents of the University of Colorado. In this document, as called for in the Joint Venture Agreement, we provide the following: (1) A summary of the work completed during the period encompassed by Phase 1 as described in the Work Plan submitted to the Forest Service on October 17, 2000, and (2) A description of field studies and other related tasks to be conducted during Phase 2 of the Joint Venture.

**A. INTRODUCTION**

Ponderosa pine (*Pinus ponderosa*) has the largest geographic range of any conifer in North America (Baumgartner and Lotan 1988). Ponderosa pine ecosystems dominate much of the montane West, and are of tremendous ecological and economic importance. Parasites and herbivores pose formidable challenges to plant fitness generally (e.g. Howe and Westley 1998; Fritz and Simms 1992), and to ponderosa pine specifically (Furniss and Carolin 1977; Baumgartner and Lotan 1988; Hawksworth and Wiens 1996). Innate resistance represents one important line of defense against such natural enemies (Howe and Westley 1988; Fritz and Simms 1992). A second and perhaps equally important source of protection is provided by those predators that keep such natural enemies in check according to the adage that "the enemy of my enemy is my friend" (Hairston et al. 1960). The goals of the research for this Joint Venture has been to investigate the effects of predators on ponderosa pine herbivores and to investigate how parasite-induced changes in ponderosa pine morphology affects the assemblage of arthropod predators residing in pine canopies.

The efficacy of predators as protectors of plants likely depends on many factors, the most important of which may be the composition of the predator assemblage. Predator assemblages vary in the protection they provide plants from herbivores because individual predator taxa can vary in effect strength. In addition, interactions *among* multiple predators in an assemblage can change their combined effect strength such that as an assemblage, predation strength may be greater or less than the sum of the predator's individual effects (Sih et al. 1998).

We are conducting two separate lines of inquiry investigating predator assemblages in ponderosa pine forests. Southwestern dwarf mistletoe (*Arceuthobium*

*vaginatum* ssp. *cryptopodum* (Engelm.) Hawksw. & Wiens) is an important parasite of ponderosa pine throughout the Intermountain West. This dwarf mistletoe can cause radical changes in pine morphology, including branching pattern, branch shape and needle length (Hawksworth and Wiens 1996), and colloquially such misshapen, parasitized branches have been referred to as “brooms” or “witch’s brooms”. We hypothesized that such changes in pine branch structure likely affect the canopy arthropod community, including the assemblage of arthropod predators. We collected the arthropods from parasitized and non-parasitized pine branches, and recorded branch morphological measurements in order to determine (1) whether dwarf mistletoe parasitism leads to changes in pine canopy arthropod assemblages and (2) what morphological characteristics associated with dwarf mistletoe parasitism are associated with such changes.

Our second line of inquiry investigates the role of birds and ants in the community ecology of pine canopies. Birds (Askenmo et al. 1977; Otvos 1978; Gunnarsson 1983; Hogstad 1984; Riechert and Hedrick 1990; Wise 1993; Marquis and Whelan 1994) and ants (Petal 1969; Kajak et al. 1972; Howard and Oliver 1978; Haemig 1992; Wise 1993; Aho et al. 1997; Halaj et al. 1997) have long been recognized as effective predators of arthropods in many ecosystems, including coniferous tree canopies. There is also some evidence that bird and ant predation of herbivores can provide benefit to forest trees (Skinner and Whittaker 1981; Fowler and Macgarvin 1985; Warrington and Whittaker 1985; Mahdi and Whittaker 1993; Marquis and Whelan 1994). While the individual effects these predators directly on arthropods and indirectly on trees has received attention, no work to-date has investigated whether the interactions between birds and ants changes the net effect of this predator assemblage. To investigate this possibility we initiated a factorial experiment of bird and ant exclusion to determine their individual and combined effects on pine arthropods, and a series of related experiments to characterize the nature of the interactions between birds and ants.

## **B. THE FIELD SITE AND EXPERIMENTAL SYSTEM**

### *Field site*

This work is being conducted at the Manitou Experimental Forest, an administrative unit of the USDA Forest Service Rocky Mountain Experiment Station. This site, located in Woodland Park, Colorado (39°00 N, 105°19 W), occupies 6730 ha, and our work was conducted at an elevation of 2400 m.

### *Dwarf mistletoe*

Southwestern dwarf is a common parasite of ponderosa pine (*Pinus ponderosa* var. *scopulorum* Laws.) in these forests. Where parasitism is severe, pine morphology is radically altered (Hawksworth and Wiens 1996) and branches often take a broomed shape. The stands where our work on dwarf mistletoe is conducted are approximately composed of a single cohort of 70 years pines of approximately 10 m in height.

### *Predators: Ants and birds*

The gravel-dome mounds of *Formica fusca* L. (Greg 1963) occur near the bases of ponderosa pines in this forest at a density that sometimes exceeds 125 per hectare (Mooney unpublished data), and in these areas *F. fusca* is the only ant found on ponderosa pine (Mooney pers. ob). The guild of foliage-gleaning birds at Manitou is dominated by Mountain chickadees (*Parus gambeli*) and nuthatches (*Sitta carolinensis*, *S. pygmaea*, and *S. canadensis*).

A review of dietary literature reveals that chickadee (*Parus* spp.) and nuthatch (*Sitta* spp.) prey are composed principally of lepidopterans, followed closely by flying hymenopterans, and coleopterans, and more distantly by spiders, psocopterans, homopterans, and others (Dahlsten and Copper 1979; Grundel and Dahlsten 1991; Pravosudov et al. 1996; Block and Finch 1997). There is little evidence to suggest that these birds prey on formicid ants to a significant degree, despite ample opportunity (Dahlsten and Copper 1979; Pravosudov et al. 1996; Mooney pers. ob.). *F. fusca* feed on nearly all orders of arthropods commonly found in pine canopies, i.e. they have a prey base very similar to that of the birds (Mooney unpublished data). While these birds and ants may not interact as predator and prey, there is evidence from studies on their congeners of bi-directional interference competition, i.e. birds interfere with ant foraging (Haemig 1997), and ants interfere with bird foraging (Haemig 1992, 1994, 1999). This predator-predator interaction makes it likely that the combined effects of bird and ant predation will be less than that predicted based on the two individual effects (Sih et al. 1998).

While birds and ants are effective predators of some arthropod herbivores, *F. fusca*, like many ants (Holldobler and Wilson 1990), commonly displays aggressive defense of some homopterans so as to guarantee their access to honey dew (so-called "tending") (Mooney pers. ob.). *Cinara* spp. (Homoptera: Aphididae) are abundant in pine canopies, and *F. fusca* opportunistically tend these aphids (Mooney, pers. ob.). This mutualism adds a level of complexity to the canopy community in that ants have a positive effect on those herbivores they tend.

### **C. EFFECT OF DWARF MISTLETOE ON CANOPY ARTHROPOD COMMUNITY**

#### *Introduction.*

The purpose of this work was to document the effects of dwarf mistletoe on the pine canopy arthropods. The prediction was that branches parasitized by dwarf mistletoe will have significantly different arthropod communities than non-parasitized branches because of differences in the two branch morphologies.

#### *Methods.*

We selected 10 pairs of parasitized and non-parasitized branches ranging in length from 1.4 m to 2.0 m in length. Branches within pairs were selected from separate, but neighboring trees, and were chosen to be of similar size. All pairs were selected within a 3 ha section of Manitou with high rates of dwarf mistletoe parasitism. We have noticed that the morphology of parasitized branches leads to an accumulation of needles. To determine whether such accumulations affect branch arthropod communities we removed the dead needles accumulated on each branch, collected and preserved the arthropods associated with those needles, and later weighed them in the laboratory. Next, we collected and preserved arthropods from all branches by beating them over drop cloths in a standardized fashion. All arthropods were preserved in 75% ethanol. We then recorded branch length, width, height, diameter, and compass bearing (i.e. which side of the tree the branch was on), total branch mass, foliage-free mass, foliage mass, and branch age. We also counted the number of "branch crosses" or points where two branchlets touched each-other within each branch. Parasitized branches generally have a less linear and more twisted morphology, and this measure quantifies this to a certain extent.

For each branch we have the collection of dead needle-derived arthropods and those from the remainder of the branch (i.e. 2 samples per branch). This project thus

generated a total of 40 arthropod samples (i.e. 10 pairs x 2 branches/pair x 2 arthropod collections / branch = 40 samples).

We began, but have not completed processing these samples. We selected voucher specimens of the arthropods found on these branches and they are being identified by staff of the University Museum and the Denver Museum of Nature and Science. When these vouchers are identified and samples processing is completed, we will perform ANCOVA testing for variation in the abundance of each taxonomic group of arthropods between parasitized and non-parasitized tree branches (Zar 1999). We will use branch morphological characters as covariates in these analyses. These tests will allow us to ask (1) whether the arthropod communities on these two classes of branches have the same linear relationships with each of a suite of branch morphological characters? For example, is the linear relationship between the abundance of *Cinara* spp. aphids and foliage mass the same for parasitized and unparasitized branches? If the linear relationships do not differ significantly, we can then ask (2) whether parasitized and unparasitized branches differ in arthropod abundances when influence of the morphological measures is controlled for. For example, if we statistically control for the effect of foliage mass on *Cinara* spp. abundance, do parasitized and unparasitized branches differ in the abundance of this arthropod?

### Results.

Mean morphological measurements for parasitized and non-parasitized branches are listed in Table 1. There were not statistically significant differences among parasitized and non-parasitized branches except in the number of crosses ( $F_{1,19}=68.56$ ,  $P<0.0001$ ) and mass of dead needles held by branches ( $F_{1,19}=11.8$ ,  $P=0.003$ ). As mentioned above, we have not yet finished processing the arthropod samples from this experiment.

Table 1. Parasitized and non-parasitized branch morphological measurements and ANOVA results testing for differences between the two branch types.

	non-parasitized branches	parasitized branches	test for differences between branch types	
measurements	mean (SD)	mean (SD)	F <sub>1,19</sub>	P
length (m)	1.92 (0.33)	1.69 (0.24)	3.32	0.085
width (m)	1.63 (0.75)	1.54 (0.32)	0.12	0.7333
height (m)	1.13 (0.30)	1.07 (0.26)	0.22	0.6427
diameter (mm)	54.0 (6.7)	59.0 (8.9)	2.02	0.1726
crosses (#)	0.00 (0.00)	6.3 (2.4)	68.56	<0.0001
bare mass (g)	2678 (1398)	3785 (1693)	2.54	0.1281
foliage mass (g)	2344 (1870)	1720 (894)	0.91	0.3535
total mass (g)	5002 (2718)	5505 (2514)	0.17	0.6845
branch age (yr)	26 (11.8)	34.5 (8.8)	3.35	0.0838
needles (g)	4.60 (14.45)	159.84 (142.2)	11.8	0.003

### Discussion.

Because we have not yet processed arthropod samples there are no conclusions yet from this experiment. We would like to note, however, that during the field collection of arthropods we perceived a higher abundance of pseudoscorpiones, adult

beetles, and a single morpho-species of spider from the parasitized branches, and it was our impression that these were associated with the accumulations of dead needles such branches collect.

#### *Phase 2 Tasks.*

1. Complete the identification and processing of the arthropod samples.
2. Perform statistical analyses on these data, as described above.
3. Report results in the form of publication and/or oral presentation.

In addition to completing the work begun under Phase 1, we will begin the following experiment:

4. Establish manipulative field experiment investigating the mechanisms of dwarf mistletoe effects on canopy arthropod communities. We will construct “artificial” dwarf mistletoe brooms from non-parasitized branches by securing dead wood and stocking these artificial brooms with bunches of dead pine needles. We will match these artificial brooms with un-manipulated brooms and unbroomed branches.
5. At the conclusion of the summer we will collect the arthropods from all branches.
6. Identify all arthropods from Task 5 above.
7. Perform statistical analyses .
8. Report results in form of publication and/or oral presentation.

### **D. EFFECTS OF BIRDS AND ANTS ON CANOPY ARTHROPOD COMMUNITY**

#### *Introduction.*

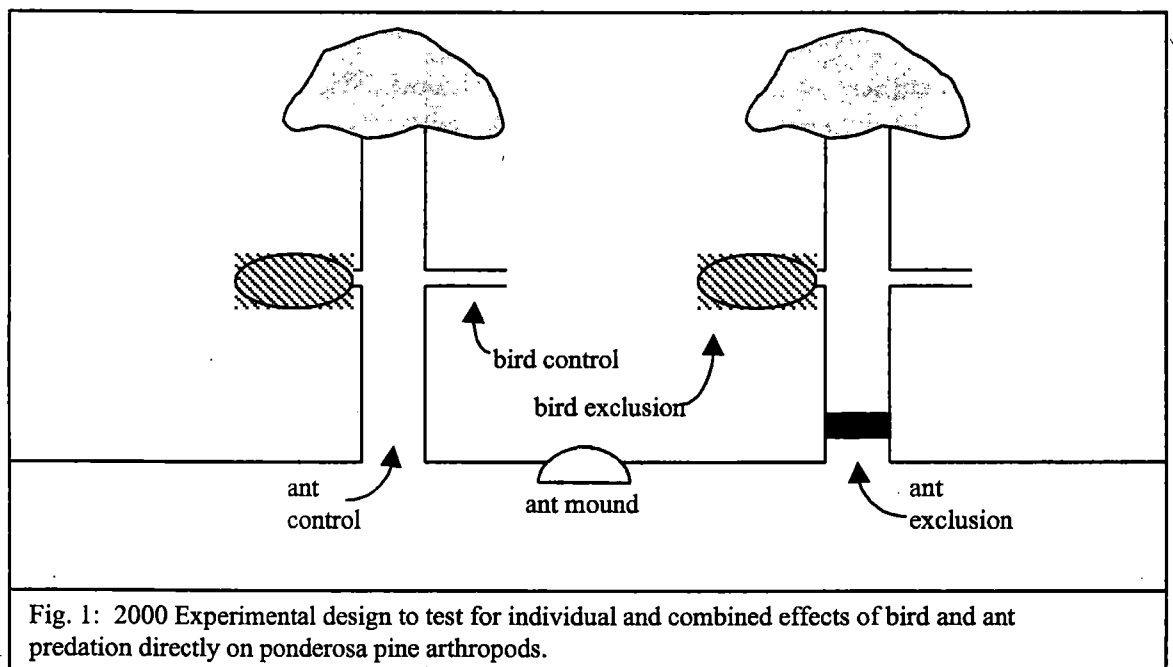
The purpose of this experiment was to determine the individual and combined effects of bird and ant predation on the ponderosa pine canopy arthropod community.

#### *Methods.*

In June of 2000 we initiated a factorial experiment of bird and ant exclusion in ponderosa pine canopies (Fig. 1). We selected 16 pairs of trees closely associated with identified mounds of *F. fusca*. We manipulated one tree from each pair with an ant exclusion treatment (a sticky barrier around tree bases), selected pairs of branches on both trees, and then manipulated one branch from each pair with a bird-exclosure (2.5cm-opening mesh bags). These treatments generate a two-by-two factorial design such that each pair of trees included branches in each of the following four treatments: ant-exclusion, bird-exclusion, ant and bird exclusion, and controls. All tree-pairs were more than 200 m apart for statistical independence, while trees within pairs were separated by an average of 4.9 m (SD=1.8). Trees averaged 9.2 m in height (SD=3.0), branches averaged 1.8 m in length (SD=0.34), and ant mounds were an average of 2.6 m (SD=1.9) from tree bases.

We collected arthropods from all branches by beating them over drop cloths in a standardized fashion and preserving them in 75% ethanol. We made these collections at in early August and mid-September. After preliminary trials we found a one month interval to be long enough for branch recolonization, as have others in similar experiments (e.g. Halaj 1997).

Both predator exclusions were successful. While the bird exclusion is permeable to all arthropods, the ant barrier also excludes other arthropods that use the tree trunk to access the canopy. To identify which canopy-taxa are affected, we placed pitfall and sticky-trap on the trunks of all trees. Other studies excluding ants in spruce (Haemig



1992, 1994) and Douglas-fir forests (Halaj 1997) found that despite these unintended consequences of ant exclusion, sticky barriers resulted in large *increases* in overall arthropod abundance.

All arthropods were sorted at least to the taxonomic level of Order, in some cases family (e.g. lepidopteran larvae), and we are identifying aphids (Aphididae: Homoptera) to the generic level. For every arthropod we also record its size to the nearest millimeter. Figure 2 shows a sample arthropod sorting form.

We tested for the effect of birds, ants, and for interaction between the two predators using a multi-factor, repeated measures ANOVA with bird, ant, and time treatments as fixed effects and tree-pair as a random block effect. Each test for main effects and the test for statistical interaction are made over the appropriate error terms (Zar 1999). We tested separately for main effects of ant and bird treatments, and for interaction between these two manipulations on two genera of aphids (*Cinara* spp. and *Esigella* spp.), spiders, lepidopteran larvae, hemipterans, 'other predators' (thysanopteran, coleopteran, neuropteran, and pseudoscorpian larvae and pseudoscorpian and coleopteran adults), and 'other herbivores' (mites, Colembola, and Psocoptera). For those tests for which there were not significant treatment effects or interactions between treatments we performed post-hoc power analyses and determined minimum detectable differences for treatment effects for a power level of 0.80 (Zar 1999). We performed these power analyses both for a sample size of 16 branches per treatment (the current design) and for an expanded sample size of 20 branches per treatment (proposed below under *Phase 2 Tasks*).

We also tested for the effects of bird enclosure on ant abundance. In this one instance, we analyzed the data as a fully randomized (i.e. not a blocked) design. We felt justified in a different approach for this specific test for the following reason - Experimental trees were selected for this work specifically based on the presence of *F. fusca* mounds, where the abundance of all other arthropods were determined by ambient environmental conditions and treatment effects. For non-ant arthropods, the prediction of significant spatial variation in abundance over the study site was our rationale for a block design. However, because trees were selected specifically for the presence of ants, spatial variation among experimental trees in ant abundance is considerably lower and therefore *a priori* justifies a different, and more powerful statistical approach in which the data are analyzed as a randomized design.

## Results.

Across all treatments there was a mean of 180 arthropods per branch (SE=31). Mean branch foliage mass was 1230 g (SE=55) and there were a mean of 160 (SE=32) arthropods per kilogram of branch foliage.

The results from all ANOVAs testing for differences among bird and ant treatments are listed in Table 2, and the means and standard errors for each taxonomic group are shown in Figures 3-10. Both birds and ants had significant effects on *Cinara* spp. aphids, and there was significant interaction between the two effects. Birds reduced and ants increased *Cinara* abundance, but the effects of birds was only present in the presence of ants. There were not significant effects of any manipulations on *Esigella* nor on spiders, lepidopteran larvae, or other predators (Thysanoptera, Neuroptera, Pseudoscorpiones, Coleoptera). Ants had a marginally significant, negative effect on hemipterans. Ants a significant effect and birds had a marginally significant effect on other herbivores (Colembola, Psocoptera, Acari), and there was no significant interaction between birds and ants. Birds had a significant negative effect on ant abundance.



Sample: 8AC - 8/11		Date Sorted: 3/5/2001				By: Jan Halach	
Vials: unknown [ ] ; Araneae [x]; other [x]; photo [ ]		Time:					
50cc: Y/N	0-1mm	1-2mm	2-3mm	3-4mm	4-5mm	>5mm	Total
Aphididae Cinara	525 12	(50) 27 (55) 37 531 161	9				182
Aphididae Eragilla [ ]	4	(50) 2	74				
Homoptera (other)							
Araneae	1	611 9	2 2				12
Acari	51						
Hemiptera (nymph)							
Hemiptera (adult)				2	1		
Coleoptera adult B=blk, G=gold							
Coleoptera larva			1	1	1		
Lepidoptera larva G=Geometridae					1	6 1	2
Formica sp.	1						
Hymenoptera (other)							
Psocoptera			1				
Pseudoscorpiones							
Neuroptera		2					
Thysanoptera		1					
Collembola		1					
Diptera	1	1					
Unknown (no wing)							
Unknown (wing)							
Total							

#s are single digit unless circled; #s in ">5mm" category are the sizes not #s of individuals; # in box = winged, otherwise wingless; sub-types within rows (indicated in column 1) denoted by LETTER=#

Figure 2. Arthropod sorting form, showing taxonomic and size categories.

Table 2. Results from repeated measures ANOVAs testing for main effects of bird and ant predation, and interaction between the two. Sample sizes for this experiment was 16 branches per treatment (i.e. 16 blocks of 1 branch in each treatment).  $1-\beta$  is the power of the test performed.  $\delta$  is the estimated difference detectable between treatments as a percentage of the grand mean for listed sample sizes ( $n=16$ ,  $n=20$ ).

<b><i>Cinara spp.</i></b>					
Source	$F_{1,15}$	P	$1-\beta$	$1-\beta = .80$ $\delta(n=16)$ $\delta(n=20)$	
bird	29.34	.0001	.99	60	54
ant	10.32	.0058	.84	99	88
bird x ant	5.17	.0381	.55	--	--

<b><i>Esigella spp</i></b>					
Source	$F_{1,15}$	P	$1-\beta$	$1-\beta = .80$ $\delta(n=16)$ $\delta(n=20)$	
bird	1.54	.2341	<.30	18	16
ant	0.00	.9898	<.30	38	33
bird x ant	0.21	.6532	<.30	--	--

<b><i>Araneae</i></b>					
Source	$F_{1,15}$	P	$1-\beta$	$1-\beta = .80$ $\delta(n=16)$ $\delta(n=20)$	
bird	0.13	.7230	<.30	33	30
ant	1.35	.2640	<.30	39	35
bird x ant	0.22	.6461	<.30	--	--

<b><i>Larval Lepidoptera</i></b>					
Source	$F_{1,15}$	P	$1-\beta$	$1-\beta = .80$ $\delta(n=16)$ $\delta(n=20)$	
bird	1.35	.2630	<.30	62	55
ant	2.00	.1782	<.30	53	47
bird x ant	1.31	.2697	<.30	--	--

<b><i>F. fusca</i></b>					
Source	$F_{1,15}$	P	$1-\beta$	$1-\beta = .80$ $\delta(n=16)$ $\delta(n=20)$	
bird	5.13	.0253	.53	118	106
ant	--	--	--	--	--
bird x ant	--	--	--	--	--

<b><i>Hemiptera</i></b>					
Source	$F_{1,15}$	P	$1-\beta$	$1-\beta = .80$ $\delta(n=16)$ $\delta(n=20)$	
bird	0.17	.6866	<.30	63	56
ant	3.36	.0867	<.30	92	82
bird x ant	0.29	.5961	<.30	--	--

<b><i>Other predators</i></b>					
Source	$F_{1,15}$	P	$1-\beta$	$1-\beta = .80$ $\delta(n=16)$ $\delta(n=20)$	
bird	2.04	.1741	<.30	68	61
ant	0.16	.6965	<.30	110	98
bird x ant	0.77	.3947	<.30	--	--

<b><i>Other</i></b>					
Source	$F_{1,15}$	P	$1-\beta$	$1-\beta = .80$ $\delta(n=16)$ $\delta(n=20)$	
bird	3.33	.0880	.35	22	19
ant	4.69	.0469	.42	44	39
bird x ant	0.63	.4396	<.30	--	--

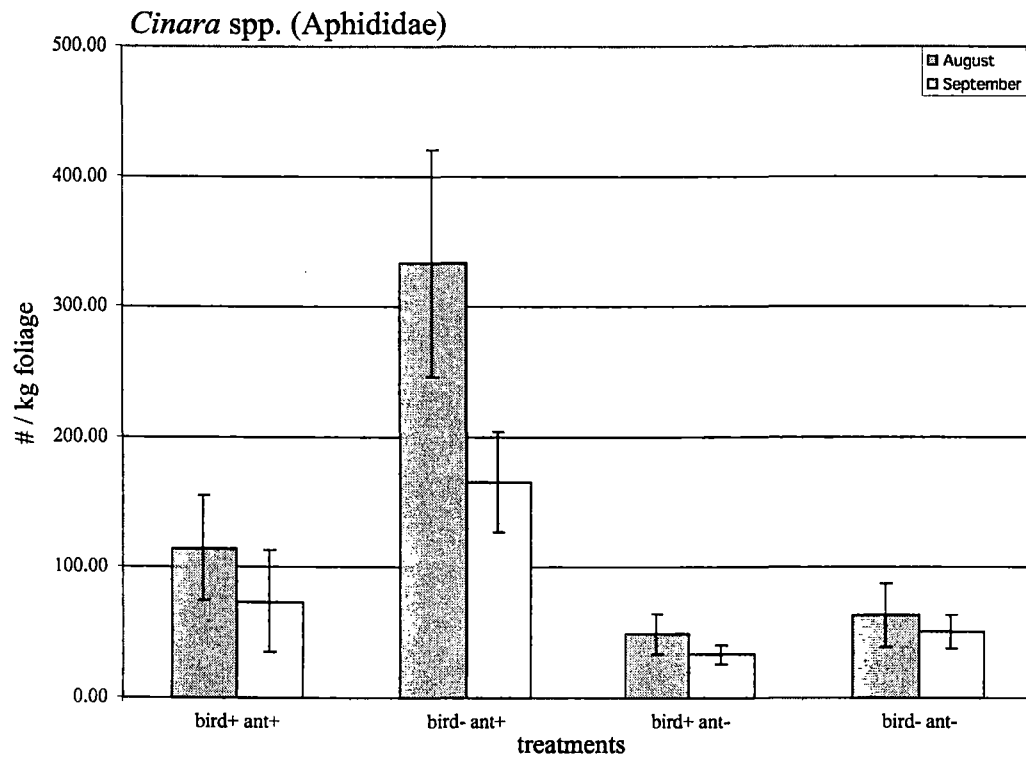


Figure 3. Mean *Cinara* spp. aphid abundance in four treatments, and two sampling periods. Bars show  $\pm$  1 SE.

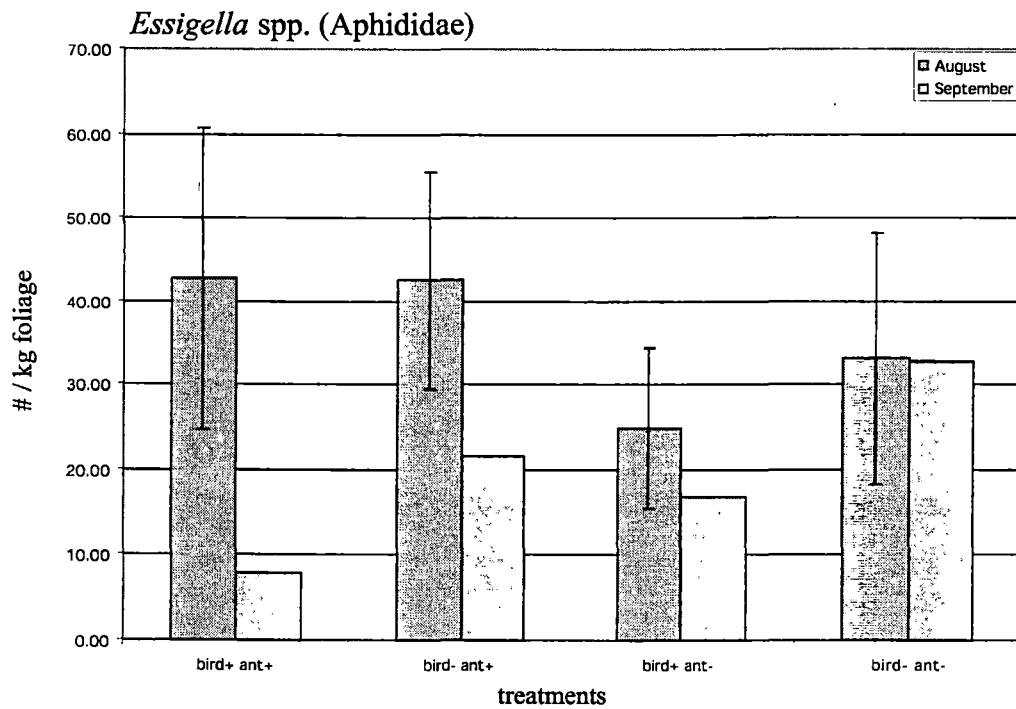


Figure 4. Mean *Essigella* spp. aphid abundance in four treatments, and two sampling periods. Bars show  $\pm$  1 SE.

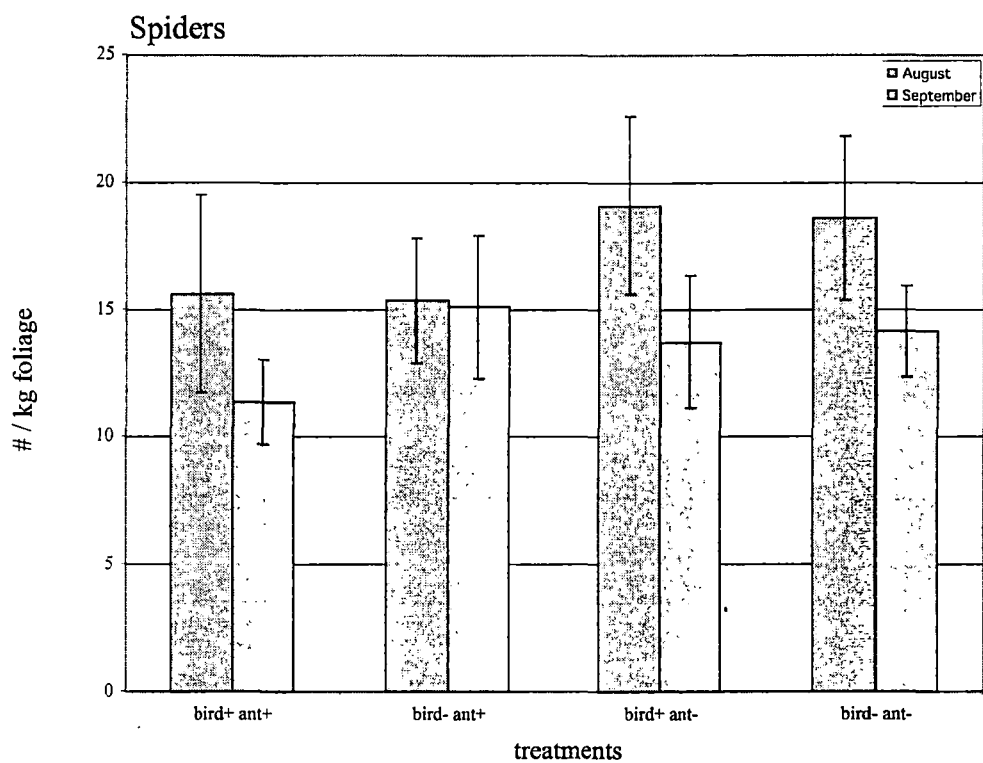


Figure 5. Mean spider abundance in four treatments, and two sampling periods. Bars show  $\pm 1$  SE

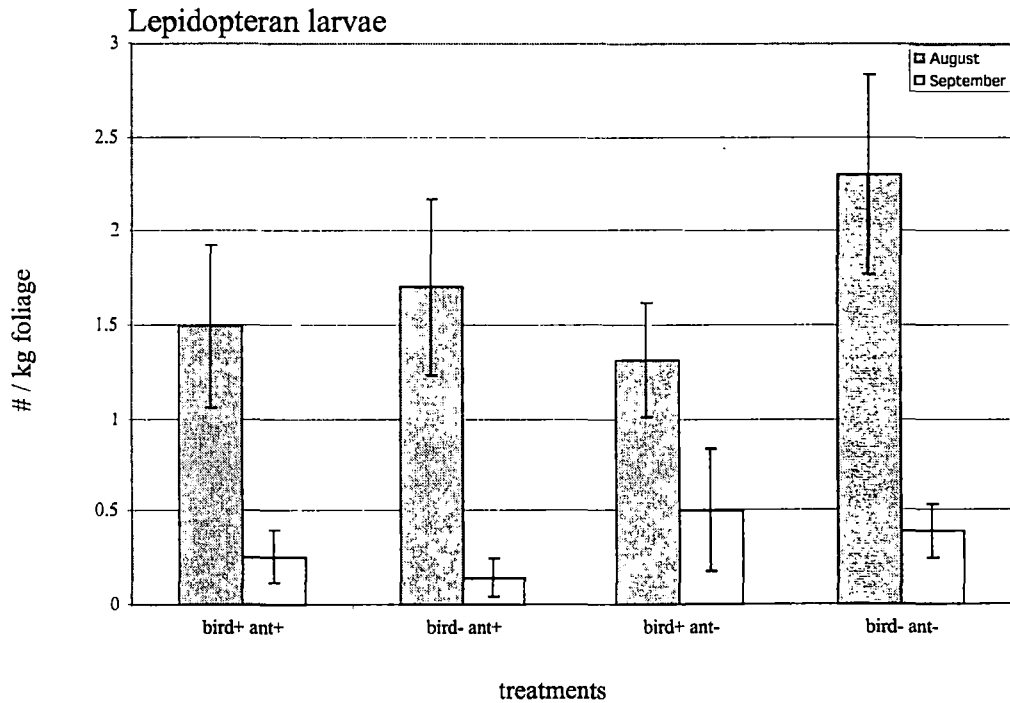


Figure 6. Mean lepidopteran larvae abundance in four treatments, and two sampling periods. Bars show  $\pm 1$  SE

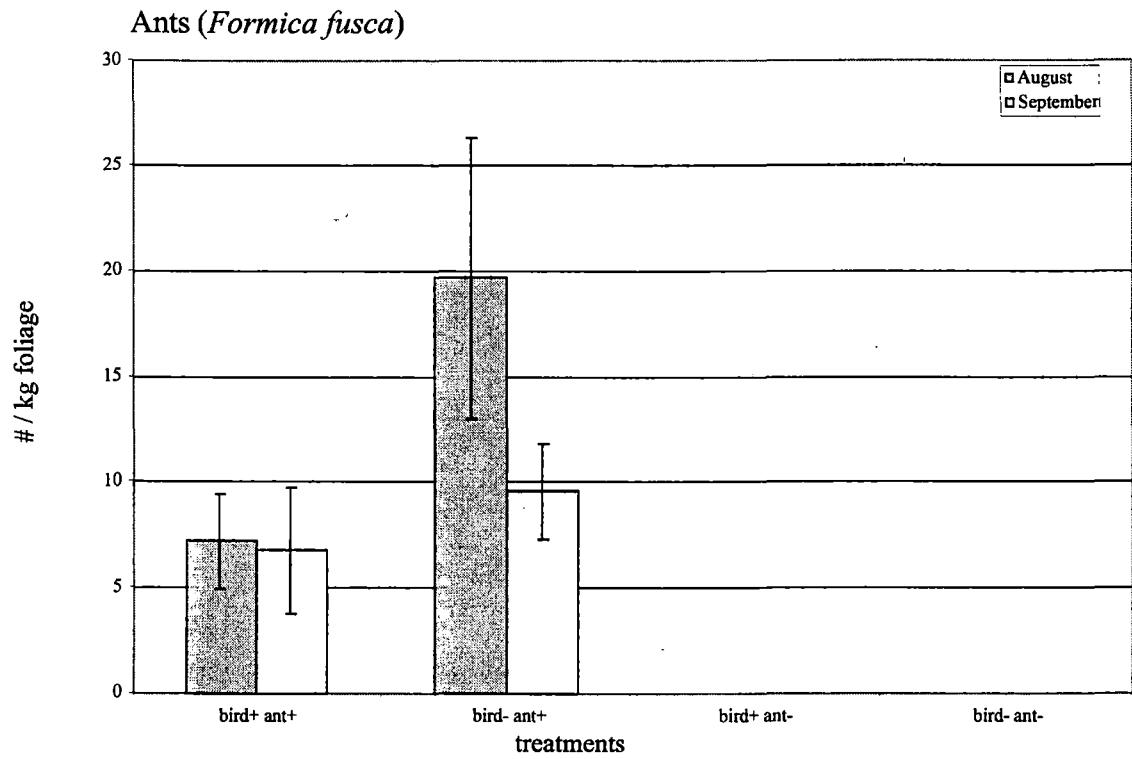


Figure 7. Mean ant abundance in four treatments, and two sampling periods. Bars show  $\pm$  1 SE

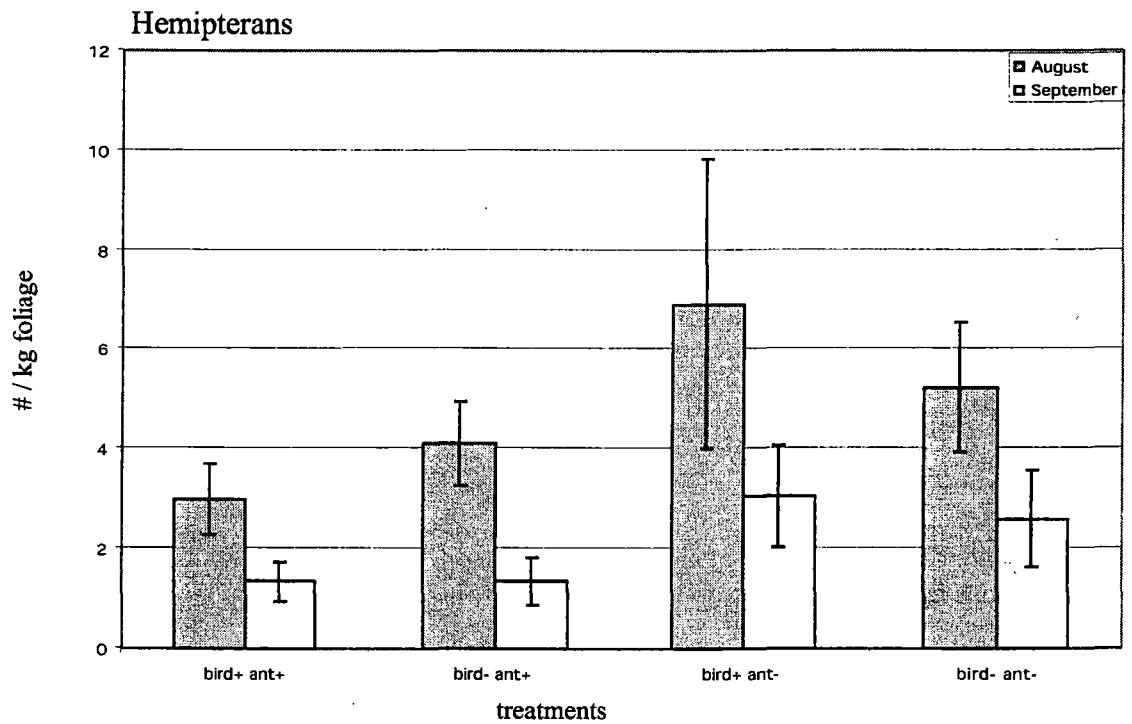


Figure 8. Mean hemipteran abundance in four treatments, and two sampling periods. Bars show  $\pm$  1 SE

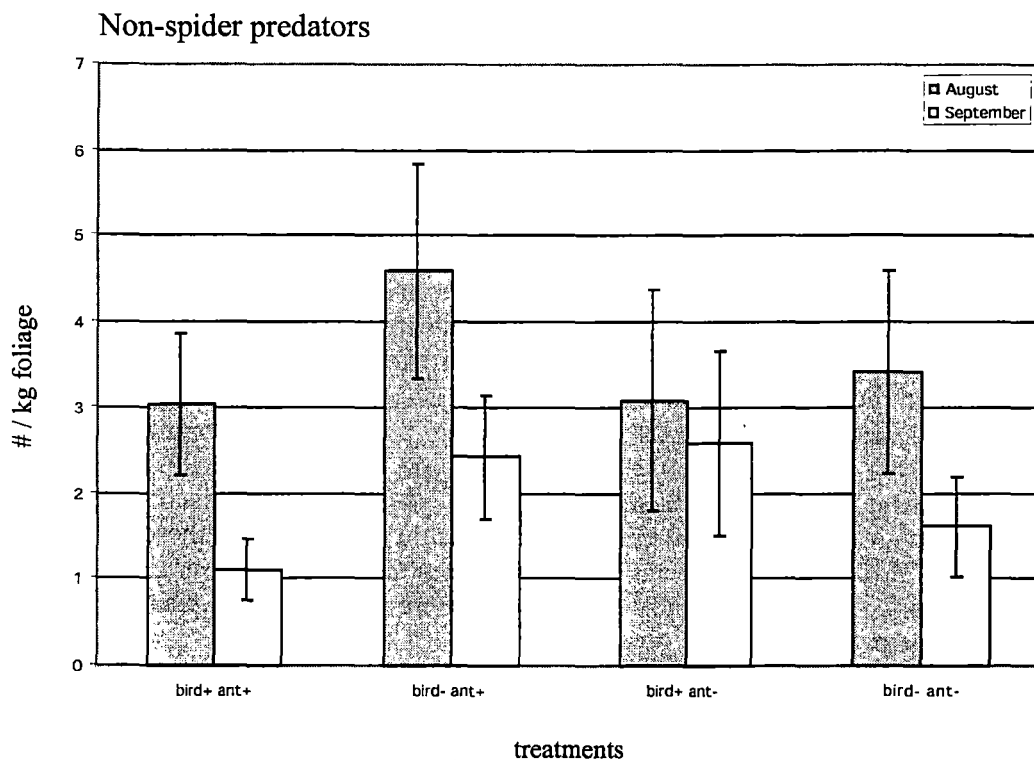


Figure 9. Mean non-spider predator abundance in four treatments, and two sampling periods. Bars show +/- 1 SE. (Coleopteran, thysanoptera, and neuropteran larvae; Pseudoscorpiones).

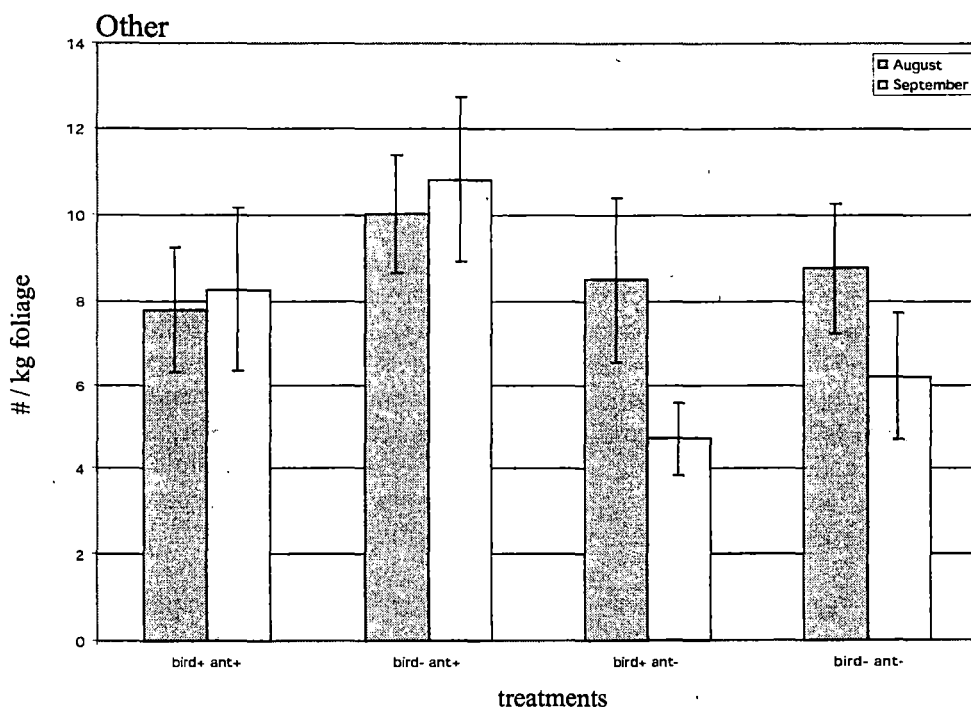


Figure 10. Mean "other" abundance in four treatments, and two sampling periods. Bars show +/- 1 SE. (Psocoptera, Acari, non-Aphididae homopterans, un-winged unknowns).

### *Discussion.*

Ants increase *Cinara* aphid abundance, but have no effect on *Esigella* aphids. This finding implies that ants tend *Cinara* but not *Esigella* aphids on ponderosa pine. Birds have negative effects on *Cinara* in the presence of ants, but not in their absence, and in neither case do birds affect *Esigella* aphids. These findings together suggest that the negative effect of birds on aphids is due to an effect of birds on the ant-aphid mutualism, and not due to a direct effect of birds on aphids. This effect could be due to bird predation or interference competition with ants (ants are less abundant in the presence of birds), or birds might somehow disrupt the ant-aphid mutualism and in doing so reduce the abundance of both. For example, mechanical disturbance can result in greater aphid mobility and thus a decrease in the efficacy of ant tending, and foraging birds might lead to such an effect without actually preying on either ants or birds.

It was surprising to us we did not see stronger effects of birds and ants on other arthropod taxonomic groups. While the minimum detectable difference for these tests are somewhat high (see Table2), the treatment effects we anticipated based on our extensive reading of the literature often substantially exceed the differences for which we had the statistical power to detect.

### *Phase 2 Tasks.*

1. We will continue our work investigating the effects of birds and ants on the pine canopy arthropod community with one significant change. Our 2000 our design was a split-plot where the bird treatment was nested within the ant treatment (Fig. 1). It has come to our attention that there may be biological interactions between the arthropod communities among branches within trees, and we believe it is possible there could be unintended interactions between treatments nested within the same tree. For example, bird exclosure branches may serve as a source of arthropods increasing the abundance on control branches. Alternatively, the presence of enemy-free space within bird exclosures could reduce the abundance of certain arthropods on control branches. Because pairs of treatments are consistently associated with each other (i.e. the no-ant treatments with and without birds are always on one tree and the ant-control treatments with and without birds on the other tree), such biological interactions between treatments potentially confounds the interpretation of our results. To remedy this situation we will add two additional trees to each existing pair and switch from the current tree-pair design (Fig. 1) to a one-treatment-per-tree scenario (Fig. 11-A). In addition, we will increase the sample size for this experiment from 16 branches per experimental treatment to 20 branches, and we will sample four times during the summer of 2001. The estimated minimum detectable differences for a sample size of 20 branches and two sampling periods are provided in Table 2. These estimates are very conservative because we will be four, not two sampling periods.
2. In 1999 16 whole-tree bird exclosures were constructed, and each tree was paired with a nearby control. This summer, for the third and last time, we will perform visual surveys (1 per month = 4) of pine arthropod fauna on these trees. In addition, early in the field season we will collect foliage herbivory data from needles flushed in 2000. We will also repair and maintain these bird exclosures as needed.

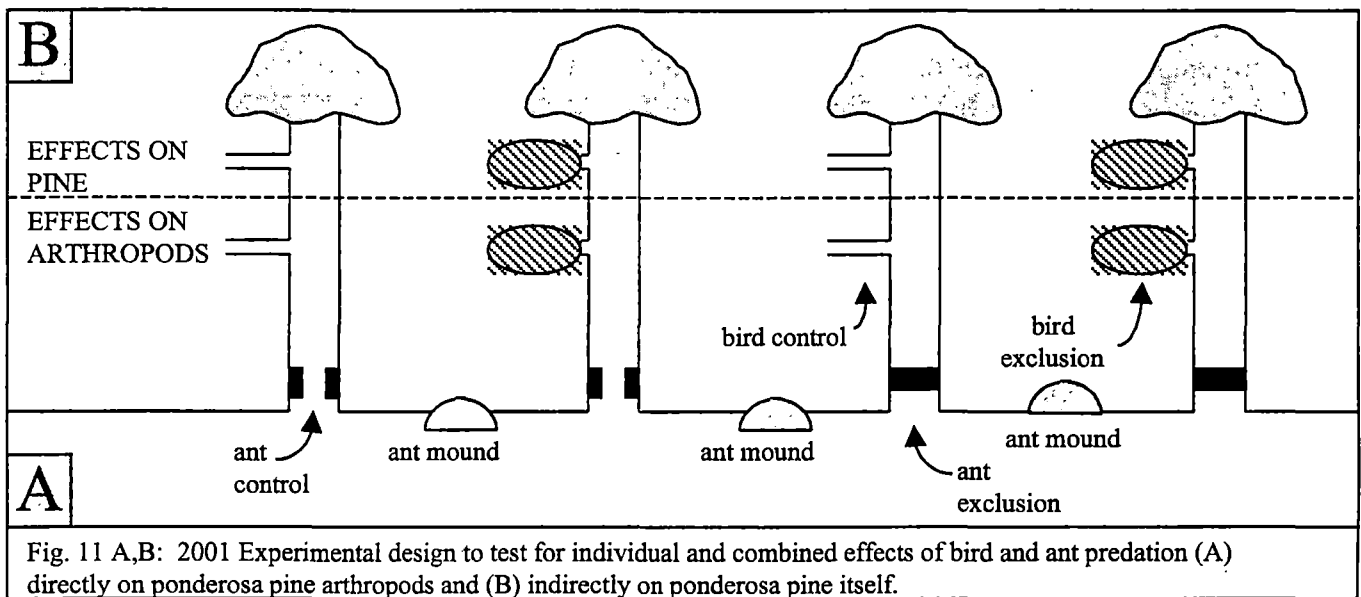


Figure 12. Artificial, clay covered branch used to record tracks of birds foraging in ponderosa pine trees. Inset shows bird tracks.



## E. EFFECTS OF ANTS ON AVIAN FORAGING

### Introduction.

The goal of this experiment was to determine whether ants affect the behavior of canopy foraging birds. This work is an important companion experiment to our work investigating the effects of birds and ants on canopy arthropods (described above in section F) as it elucidates the interactions between the two predators in this system.

### Methods.

This experiment used the same 16 pairs of ponderosa pine trees described above in section F. Each tree-pair is closely associated with a mound of the ant *F. fusca*. We excluded ants from one tree in each pair using "tangle-trap insect trap coating" (Tanglefoot Company, Grand Rapids, Michigan USA). Pairs of trees were selected to be similar in height and overall morphology.

In order to determine whether the presence of *F. fusca* affected avian foraging we observed each pair of experimental trees on multiple occasions between July 15 and September 1. We noted the species of bird foraging and the duration of each foraging event. In total we observed experimental trees for 180 hours and 4.3 bird-hours of foraging. We tested for differences in total bird visitation between ant and no-ant trees with a two-way model 2 ANOVA with ant treatment as a fixed effect and tree-pair as a random block effect (Zar 1999).

We supplemented these direct observations of experimental pairs with data from a novel tracking technique (Mooney, submitted). We constructed artificial clay-covered branches to record the claw markings of landing birds (Fig. 12). On each experimental tree we placed three artificial branches on pine branches of approximately 2.5 cm in diameter. Placements ranged from 1.5 m to 4 m in height. We let the artificial branches sit unchecked and accumulate tracks for two consecutive sampling periods of four days each between 24 August and 28 August, and 28 August and 1 September 2000. We calculated tree scores ranging from 0 (no artificial branches marked in either sampling period) to 6 (all artificial branches marked in both sampling periods). We compared the mean scores from trees with and without ants using a two-way model 2 ANOVA with ant treatment as a fixed effect and tree-pair as a random block effect (Zar 1999).

### Results.

We observed pairs of trees with and without ants for a total of 10800 minutes (180 hours) and observed a total of 255 minutes of foraging activity. Approximately 44% of all foraging was done by chickadees (*Parus* spp.), 36% by nuthatches (*Sitta* sp.), and the remaining 20% was distributed across 12 other species. We observed a mean of 342 minutes (N=16, SE=91.0) of bird foraging on trees with ants, a mean of 677 minutes (N=16, SE=169) of foraging on trees without ants, but this difference was not significant ( $F_{(1,15)}=1.41$ ,  $P=0.26$ ), indicating that birds foraging patterns are not affected by *F. fusca*. The results from our artificial branches were similar: Tree scores ranged from 0 to 5 with mean scores of 2.6 (n=16, SD=1.31) for ant trees and 2.1 (n=16, SD=1.26) for no-ant trees, and this difference was not significant ( $F_{1,30}=0.92$ ,  $p=0.34$ ) (Fig. 13).

### Discussion.

Two separate lines of evidence suggest that the presence of *F. fusca* does not alter avian foraging patterns in the canopies of ponderosa pines. Haemig (1994) found that in a Spruce forest (*Picea abies*) in Norway the presence of *F. aquilonia* significantly reduced the foraging time of several bird species, including tits (*Parus* spp.). However,

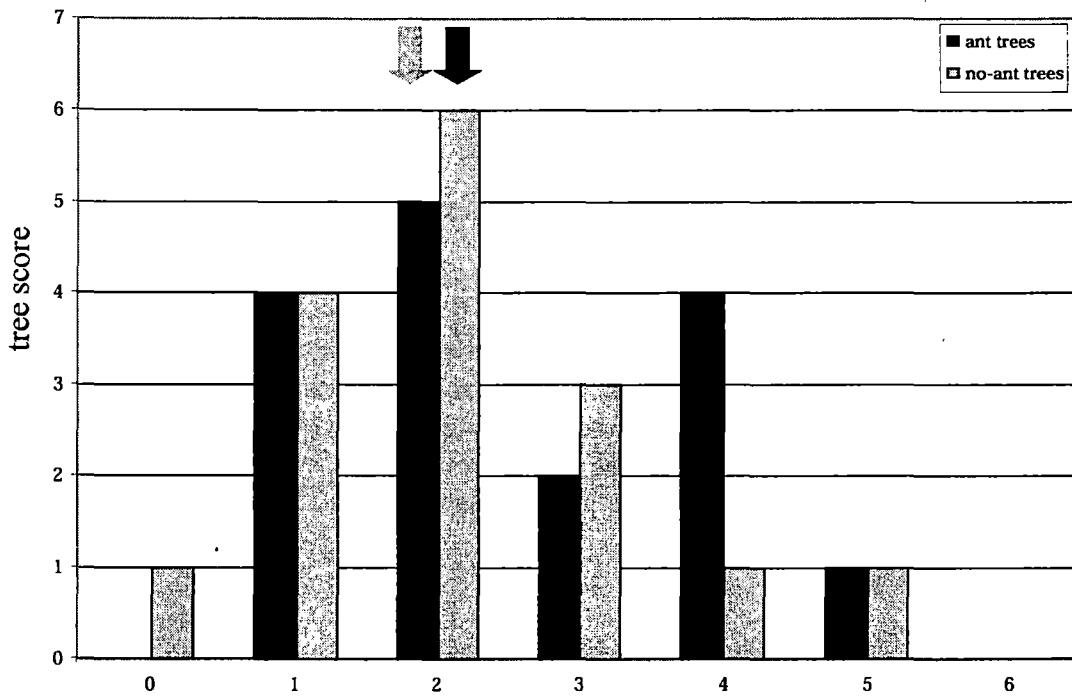


Figure 13. Frequency distribution of tree-scores from artificial branches placed on ant and no-ant trees. Arrows show the means.

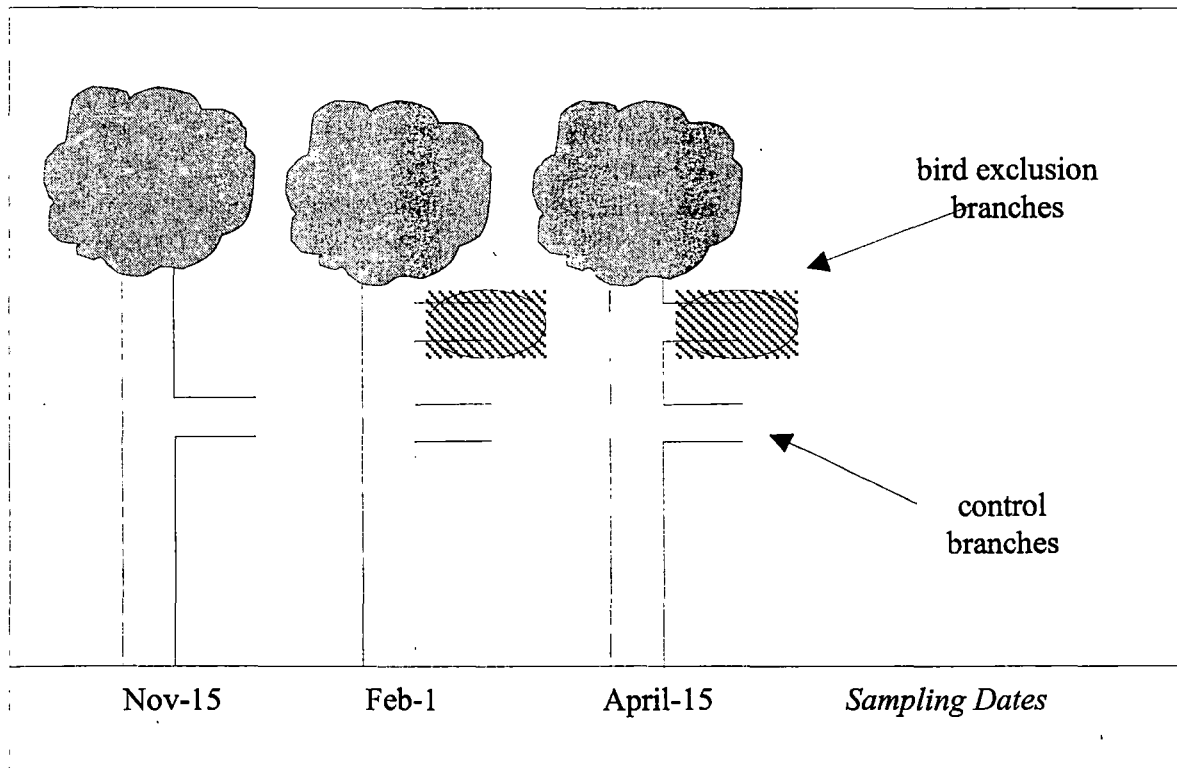


Figure 14: One pine triplet with five experimental branches. There are 10t such triplets in the full experiment.

Haemig (1994) also found these ants significantly reduced prey abundance, where we do not have evidence that *F. fusca* reduced prey abundance in this study. It is possible that differences in foraging efficiencies between the ants in Haemig's study site and our own are responsible for the discrepancies in our findings.

#### *Phase 2 Tasks.*

1. Report results in form of publication and/or oral presentation.

### **F. EFFECTS OF WINTER BIRD PREDATION ON CANOPY ARTHROPODS**

#### *Introduction.*

Many spiders over-winter as juveniles (Gunnarsson 1983; Gunnarsson and Hake 1999; Wise 1993; Foelix 1996), and past studies of coniferous forest systems have found that winter predation by birds significantly reduces spider abundance (Gunnarsson 1983; Gunnarsson and Hake 1999). The purpose of this experiment was to determine whether winter resident birds in ponderosa pine forests (*Parus* spp. and *Sitta* spp.) have similar effects.

#### *Methods.*

The planned design of this experiment was the following:

- A. Select 10 triplets of pines (Fig. 14) in mid-November.
- B. Collect all insects and spiders from one branch on the first tree in each triplet.
- C. Simultaneous with this first collection select pairs of branches on the second and third trees in each triplet. One branch in each pair will be enclosed in a 2.5cm-opening mesh bag to exclude birds. The other branches serve as controls.
- D. In early February collect all insects and spiders on the paired control and bird-exclusion branches from the second tree in each triplet.
- E. In mid-April collect from the pairs of branches on the third tree in each triplet.
- F. Count and identify the preserved spiders.

This experimental design generates a sample size of 10 unmanipulated (i.e. control) branches for each of the three sampling periods (i.e. mid-November, early-February, and mid-April), and 10 manipulated, bird-exclosure branches to be sampled in last two sampling periods (i.e. early-February and mid-April).

In November we selected the 10 triplets of trees and installed the bird exclosures as described above (step A and C). However, when we initiated branch sampling (step B) we found there were no arthropods in the ponderosa canopies. We returned and sampled non-experimental branches repeatedly through the winter, but this sampling never revealed any arthropods.

Simultaneous with these sampling efforts, we placed sticky-traps on the trunks and branches of each tree as a second means of identifying the presence of winter-active arthropods. We placed a 10cm long strip of tangle-foot stick paste on the trunk of each tree, and a second around the entire circumference of a single branch of approximately 5cm in diameter. We checked these traps in early April for arthropods.

#### *Results.*

Despite our expectation that spiders would be present in pine canopies in winter, branch sampling did not reveal spiders nor any other arthropods at any point through the winter. We checked the trunk and branch sticky traps in early April. Of 20 sticky a total of seven arthropods were captured (three spiders, two ants, two diptera).

### *Discussion.*

To our surprise, arthropods were essentially absent from ponderosa pine canopies in winter. However, we have made some observations which partially clarify this finding: (1) In early spring (mid-April) we found ants foraging in pine canopies returning to their nests with neuropteran larvae. (2) Although chickadees forage substantially in leaf litter in winter, they still dedicate a substantial foraging effort to pine canopies. These two observations lead us to believe that while arthropods, including spiders, may not be active in winter, they likely are present in bark cavities. The fact that some spiders were found in our winter sticky traps, but not in our branch samples, suggests that a few arthropods may emerge on exceptionally warm days throughout the winter. The fact that Gunnarsson (1983) and Gunnarsson and Hake (1999) found spiders active on spruce branches in winter in Norway may be due to climatic differences between study sites. However, the relatively low elevation of our site (2400m) makes it unlikely that Manitou is substantially colder than the Norwegian spruce forests where their work was conducted.

### *Phase 2 Tasks.*

1. Report results in form of publication and/or oral presentation.

## **G. INDIRECT EFFECTS OF PREDATORS ON PONDEROSA PINE**

### *Introduction.*

This is a new project to begin in Phase 2 of this Joint Venture. The purpose of this work is to determine the individual and combined indirect effects of birds and ants on ponderosa pine. This work is closely related to Section D described above, which characterized the direct effects of birds and ants on the ponderosa pine canopy arthropod community.

### *Phase 2 Tasks.*

1. Select an additional experimental branch on all experimental trees (Fig. 11-B). These branches will not be disturbed for the duration of the experiment.
2. At the conclusion of the 2001 season we will measure needle herbivory, needle length, needle density, branch elongation (primary growth) and branch increment increase (secondary growth).
3. Statistically analyze these data to test for indirect effects of predator manipulations on ponderosa pine.
4. Report results in form of publication and/or oral presentation.

## **H. EFFECTS OF BIRDS ON ANTS**

### *Introduction.*

This is a new project to begin in Phase 2. During the summer of 2000 we identified the effects of ants on birds (Section E above). The purpose of this work is to investigate the mechanisms by which birds affect ants. Ants have been shown to jump from trees to escape birds (personal observation), and it is our prediction that differences in ant abundance between bird exclusion and control branches (Section D above; Table 3; Fig. 7) may be due not to predation, but to an increase in such escape behavior.

*Phase 2 Tasks.*

1. Over the course of the summer we will count the number of ants going to and from bird exclosure and control branches and then put out the sticky traps for 24 hours.
2. Beneath the branches with and without birds we will place sticky traps suspended on a horizontal plane and count the number of ants caught per 48 hour period.
3. We will test for a difference in sticky trap capture rate of ants between bird exclosure and control branches using an ANCOVA with ant traffic as a covariate. This test will determine whether there are differences in ant jumping rate between treatments, corrected for ant abundance on each branch.
4. Report results in form of publication and/or oral presentation.

**I. DWARF MISTLETOE SEED COLLECTION**

*Introduction.*

This is a new project to begin in Phase 2. The purpose of this work is to gather seeds to be used by the Rocky Mountain Research Station in growth chamber experiments to begin in the fall of 2001.

*Phase 2 Tasks.*

1. Collect approximately 1000 seeds from *Arceuthobium americanum* parasitizing lodgepole pine (*Pinus contorta*) and *A. vaginatum* parasitizing ponderosa pine (*P. ponderosa*).

## LITERATURE CITED

- Aho, T., M. Kuitunen, J. Suhonen, A. Jantti, T. Hakkari. 1997. Behavioral responses of Eurasian treecreepers, *Certhia familiaris*, to competition with ants. *Animal Behaviour* 54: 1283-1290.
- Askenmo, C., von Bromssen, A., Ekman, J., and C. Jansson. 1977. Impact of some wintering birds on spider abundance in spruce. *Oikos* 28: 90-94.
- Baumgartner, D.M. and Lotan, J.E. Eds. 1988. *Ponderosa Pine: The Species And Its Management*. Sym. Proc., Washington State Univ., Coop. Ext. Serv., Pullman.
- Block, W.M. and D.M. Finch., Eds. 1997. *Songbird Ecology in Southwestern Ponderosa Pine Forests*. USDA Forest Service General Technical Report RM-GTR-292. 152 pp.
- Dahlsten, D.L. and W.A. Copper, 1979. The use of nesting boxes to study the biology of the Mountain Chickadee (*Parus gambeli*) and its impacts on selected forest insects. In: J.G. Dickson, R.N. Conner, R.R. Fleet, J.C. Kroll, and J.A. Jackson, Eds. *The Role of Insectivorous Birds in Forest Ecosystems*. Pp. 217-260. Academic Press, New York NY.
- Foelix, R.F. Biology of Spiders, 2<sup>nd</sup> Ed. Oxford University Press, New York. 330 pp.
- Fowler, S.V. and M. Macgarvin. 1985. The impact of hairy wood ants, *Formica lugubris*, on the guild structure of herbivorous insects on birch, *Betula pubescens*. *J. Animal Ecol.* 54:847-855.
- Fritz, R.S. and E.L. Simms 1992. *Plant Resistance to Herbivores and Pathogens*. University of Chicago Press, Chicago US.
- Furniss, R.L. and V.M. Carolin. 1977. Western Forest Insects. U.S. Department of Agriculture Forest Service, Misc. Pub. No. 1399, Government Printing Office, Washington DC. 654 pp.
- Gregg, R.E. 1963. *The Ants of Colorado*. University of Colorado Press, Boulder CO. 792 pp.
- Grundel, R. and D.L. Dahlsten. 1990. The feeding ecology of mountain chickadees (*Parus gambeli*): patterns of arthropod prey delivery to nestling birds. *Can. J. Zoo.* 69: 1793-1804.
- Gunnarsson, B. 1983. Winter mortality of spruce-living spiders: effects of spider interactions and bird predation. *Oikos* 40: 226-233.
- Gunnarsson, B. and M.Hake. 1999. Bird predation affects canopy-living arthropods in city parks. *Can. J. Zool.* 77: 1419-1428.
- Hairston, N.G., Smith, F.E. and Slobodkin, L.B. 1960. Community structure, population control, and competition. *American Naturalist* 94:421-25.
- Hawksworth, F.G. and Wiens, D. 1996. *Dwarf Mistletoes: Biology, Pathology, And Systematics*. USDA Forest Service Agricultural Handbook 709. Washington DC.
- Haemig, P.D. 1992. Competition between ants and birds in a Swedish forest. *Oikos* 65(3): 479-483.
- Haemig, P.D. 1994. Effects of Ants on the Foraging of Birds in Spruce Trees. *Oecologia* 97(1): 35-40.
- Haemig, P.D. 1996. Interference from ants alters foraging ecology of great tits. *Behavioral Ecology and Sociobiology* 38: 25-29.
- Halaj, J., Ross, D.W., and A.R. Moldenke. 1997. Negative effects of ant foraging on spiders in

- Hogstad, O. 1984. Variation in numbers, territoriality and flock size of a Goldcrest *Regulus regulus* population in winter. *Ibis* 126: 296-306.
- Holldobler, B. and E.O. Wilson. 1990. *The Ants*. Harvard University Press, Cambridge MA. 732 pp.
- Howard, F.W. and A.D. Oliver. 1978. Arthropod populations in permanent pastures treated and untreated with mirex for red imported fire ant control. *Environmental Entomology* 7: 901-903.
- Howe, H.F. and L.C. Westley. 1988. *Ecological Relationships of Plants and Animals*. Oxford University Press, New York US.
- Kajak, A., Breymeyer, A., Petal, J., and E. Olechowicz. 1972. The influence of ants on meadow invertebrates. *Ekol. Pol.* 20: 163-171.
- Mahdi, T. and J.B. Whittaker. 1993. Do birch trees (*Betula pendula*) grow better if foraged by wood ants? *J. Animal Eco.* 62:101-116.
- Marquis, R.J. and C.J. Whelan. 1994. Insectivorous birds increase growth of white oak through consumption of leaf-chewing insects. *Ecology* 75: 2007-2014.
- Otvos, I.S. 1978. The effects of insectivorous bird activities in forest ecosystems: An evaluation. In: J.G. Dickson, R.N. Conner, R.R. Fleet, J.C. Kroll, and J.A. Jackson, Eds. *The Role of Insectivorous Birds in Forest Ecosystems*. Pp. 217-260. Academic Press, New York NY.
- Petal, J. 1978. The role of ants in ecosystems. In: M.V. Brian, Ed. *Production Ecology of Ants and Termites*. Pp. 293-325. Cambridge University press, New York, NY.
- Pravosudov, V.V., Pravosudova, E.V. and E.Y. Zimireva. 1996. The diet of nestling eurasian nuthatches. *J. Field Ornithol.* 67: 114-118.
- Riechert, S.E. and A.V. Hedrick. 1990. Levels of predation and genetically based anti-predator behavior in the spider, *Agelenopsis aperta*. *Animal Behaviour* 40: 679-687.
- Sih, A., Englund, G. and D. Wooster. 1998. Emergent impacts of multiple predators on prey. *Trends in Ecology and Evolution* 13: 350-355.
- Skinner, G.J. and J.B. Whittaker. 1981. An experimental investigation of inter-relationships between the wood-ant (*Formica rufa*) and some tree-canopy herbivores. *J. Animal Eco.* 50:313-326.
- Warrington, S. and J.B. Whittaker. 1985. An experimental field study of different levels of insect herbivory induced by *Formica rufa* predation on sycamore (*Acer pseudoplatanus*) I. Lepidoptera larvae. *J. Applied Ecol.* 22:775-785.
- Wise, D.H. 1993. *Spiders in Ecological Webs*. Cambridge University Press, Cambridge UK. 328pp.
- Zar, J.H. 1999. *Biostatistical Analysis 5th ed.* Prentice Hall, NJ